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Research

Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment

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The role of climate in determining range margins is often studied using species distribution models (SDMs), which are easily applied but have well-known limitations, e.g. due to their correlative nature and colonization and extinction time lags. Transplant experiments can give more direct information on environmental effects, but often cover small spatial and temporal scales. We simultaneously applied a SDM using high-resolution spatial predictors and an integral projection (demographic) model based on a transplant experiment at 58 sites to examine the effects of microclimate, light and soil conditions on the distribution and performance of a forest herb, *Lathyrus vernus*, at its cold range margin in central Sweden. In the SDM, occurrences were strongly associated with warmer climates. In contrast, only weak effects of climate were detected in the transplant experiment, whereas effects of soil conditions and light dominated. The higher contribution of climate in the SDM is likely a result from its correlation with soil quality, forest type and potentially historic land use, which were unaccounted for in the model. Predicted habitat suitability and population growth rate, yielded by the two approaches, were not correlated across the transplant sites. We argue that the ranking of site habitat suitability is probably more reliable in the transplant experiment than in the SDM because predictors in the former better describe understory conditions, but that ranking might vary among years, e.g. due to differences in climate. Our results suggest that *L. vernus* is limited by soil and light rather than directly by climate at its northern range edge, where conifers dominate forests and create suboptimal conditions of soil and canopy-penetrating light. A general implication of our study is that to better understand how climate change influences range dynamics, we should not only strive to improve existing approaches but also to use multiple approaches in concert.

Keywords: boreal forest, canopy cover, demography, microclimate, range margin, soil

Introduction

Identifying the factors limiting species distributions and driving abundance patterns is a longstanding question in ecology (Brown 1984, Austin 2007, Elith and Leathwick 2009), that has become particularly crucial in predicting the effects of environmental



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and climate change (Guisan and Thuiller 2005, Thuiller et al. 2008). Species distribution models (SDMs) are the most common approach to study range-wide species–environment relationships. In SDMs, presence and absence data of a species are correlated with environmental variables (Guisan and Zimmermann 2000, Franklin 2009). SDMs are relatively easy to implement and can cover larger geographic areas. Further, SDMs integrate effects over longer time periods and effects of rare but important environmental conditions, e.g. cold spells or droughts (Hargreaves et al. 2014, Lee-Yaw et al. 2016). However, several limitations of SDMs have been pointed out (Austin 2007, Schurr et al. 2012, Urban et al. 2016). For example, SDMs are based on the assumption that occurrences are in equilibrium with current environmental conditions, although it is known that time lags in extinctions and colonisations are important in many systems (Schurr et al. 2007, Thuiller et al. 2014, but see Engler and Guisan 2009). SDMs are also correlative in nature and might thus yield incorrect estimates of the impact of climate if climatic variables are correlated to other unknown or unmeasured variables (Wiens et al. 2009, Guisan et al. 2017). Further, SDMs are typically based on free-air climate conditions at a coarse resolution, failing to capture the near-ground microclimates experienced by many organisms (Lembrechts et al. 2018).

To overcome some of the problems associated with SDMs, transplant experiments (TEs) have been suggested as a way to identify the factors determining species distributions (Gaston 2003, Ehrlén and Morris 2015). Main advantages of TEs are that they do not assume equilibria, and that they can extend the environmental gradient to include also conditions where the species do not currently exist (Lee-Yaw et al. 2016). Another advantage is that TEs, if including multiple life stages, enable examination of the demographic mechanisms underlying responses, i.e. how environmental variables affect different vital rates (e.g. survival, seed germination). Lastly, TEs combined with manipulative treatments can break up natural correlations between environmental variables, thus overcoming a main disadvantage with many types of correlative studies (Battisti et al. 2005). However, identifying range-limiting factors using TEs is challenging because experiments need to be replicated along sufficiently long gradients of relevant environmental factors, and maintained over a sufficiently long time to capture temporal variation in conditions. TEs have also often not included all life stages (Sheppard et al. 2014, Lembrechts et al. 2017; but see Töpper et al. 2018). This is problematic because species distributions might be limited by effects during any phase of the organism's life cycle and only integrated measures of population performance, such as population growth rates, can tell us if survival is possible at a given site. Since SDMs and TEs have different strengths and constraints and usually examine patterns at different temporal and spatial scales, an important way to increase our understanding of the factors limiting species distributions should be to combine the two approaches. Yet, such simultaneous assessments have rarely been done (but see Lee-Yaw et al. 2016, Benito-Garzón et al. 2019).

One type of questions where the simultaneous use of both methods might be particularly advantageous is how climate

change affects range margins. Range margins are expected to shift in response to rising temperatures (Thuiller et al. 2005, Chen et al. 2011, Vilà-Cabrera et al. 2019), and shifts may be most pronounced at poleward range margins (Normand et al. 2009). Climate limitations can be direct, when the marginal climate coincides with a species' physiological limit, but also indirect, acting via changes in vegetation, biotic interactions or soil conditions (Aerts 1997, Dixon 2015). For example, a climate-driven shift from deciduous to conifer-dominated forests along the southern border of the boreal forests can modify litter fall and soil conditions (Dickinson and Pugh 1974, Barbier et al. 2008, Geiger et al. 2012). Different forest types and landforms also create considerable near-ground microclimate variation (Suggitt et al. 2011, De Frenne and Verheyen 2015, Greiser et al. 2018). Due to microclimatic heterogeneity one would expect a patchy advancing front tracking global warming (Hylander et al. 2015), where species at their cold edge would occupy sites with relatively warmer microclimates (Beauregard and De Blois 2016). Thus, large-scale biogeographical predictions at range margins, based on coarse-gridded climate data, might miss that some local populations perform well (Vilà-Cabrera et al. 2019).

In this study, we explored the factors determining the distribution and performance of a perennial forest herb, *Lathyrus vernus*, at its cold range margin, using two different approaches. First, we built a SDM using high-resolution microclimate maps, as well as information about other important drivers such as forest age and forest type, to explore how environmental factors were correlated with the distribution at a regional scale. Second, we carried out an extensive TE on 58 sites with contrasting microclimate, light and soil moisture. In this experiment, we included multiple life cycle stages and integrated the effects of environmental variables on plant vital rates observed during one year using a demographic integral projection model. To separate direct effects of climate from indirect effects occurring via soil development, we included an experimental treatment with nutrient-rich soil. We asked three main questions: 1) which environmental variables explain the distribution in a SDM framework? 2) Which environmental variables affect vital rates and population growth rates in the TE? 3) Is habitat suitability derived from the SDM correlated with the population growth rate from the TE? We predicted that *L. vernus* in the study area is climate-limited and therefore responds positively to direct and indirect benefits from warmer temperatures. Because the two approaches included predictors that were associated with the same aspects of habitat suitability, we expected the predictions of the two models to largely agree.

Material and methods

Study system

Lathyrus vernus (Fabaceae) is a long-lived herb growing in mesic forests on base- and nutrient-rich soils (Ehrlén and Lehtilä 2002, Mossberg and Stenberg 2003). It accumulates

resources in rhizomes during the growing season, overwinters belowground and flowers in spring before canopy closure. The purple flowers are pollinated by bumblebees. The seeds are dispersed over relatively short distances by abruptly opening fruits (Ehrlén 2002). The species occurs in central and northern Europe and ranges to the east of the Ural Mountains (Hultén and Fries 1986). In Sweden *L. vernus* has a southern and south-eastern distribution and declines inland above 60°N, while occurring further up along the coastal regions and in some northern river valleys.

This study was carried out in a sharp transition zone separating the northern boreal forest from the southern mixed forest in central Sweden – Limes Norrlandicus (Fig. 1, Greiser et al. 2018). The area belongs to the humid cold-temperate zone with annual mean temperature ranging from ca 5°C in the south to 3°C in the north (SMHI 2017). Precipitation decreases from west (800 mm) to east (600 mm; SMHI 2017) and falls as snow during the winter months. Soil pH is high in the south-east and east of the area and decreases rapidly towards the northwest. The heavily managed forests are dominated by Norway spruce and Scots pine in the canopy layer and dwarf-shrubs, mosses and lichens in the field layer (Rydin et al. 1999). The proportion of deciduous trees is overall low (0–40%), decreasing towards the north-northwest, and reaching higher values (up to 100%) only locally on early-successional patches after selective thinning, and on richer soils. Human population density in the countryside and various agricultural practices have historically been more prevalent towards south-southeast.

Species distribution model

The area used for the SDM spanned from 58° to 61°N and from 12 to 19°E and embraced parts of the cold range margin of *L. vernus*. For the model, we considered only forested area (52 409 km², Fig. 1). We modelled the distribution of *L. vernus* by relating presence data to six environmental variables at the highest possible resolution: climate, light, proportion of conifers, forest age, bedrock pH class and soil moisture. Presence data were obtained from a citizen science database (<<https://artportalen.se/>>, accessed 16 January 2016). We used only observations from the period 2000 to 2016 with a minimum spatial accuracy of 50 m. We filtered out observations outside forests and lumped the remaining points to a maximum of one observation per 50 m grid cell (obtaining 556 presences). Pseudo-absence data were created by sampling 1000 forested background points at a distance of 1–50 km from any presence point.

We used growing degree days (GDD) as a (micro)climate variable derived from high-resolution topoclimate grids of Sweden (Meineri and Hylander 2017). Solar radiation (SR) in spring and summer was used as a proxy for light availability, and was a function of latitude and local topography (Fu and Rich 2002). We also included the proportion of conifers (SLU Forest Map 2010), assuming that it partly reflected local light availability, light seasonality and soil pH. As another estimate of site acidity, we used the pH of the underlying bedrock, classified as base-rich, neutral or acidic (bedrock map from Geological Survey of Sweden, SGU jordarter

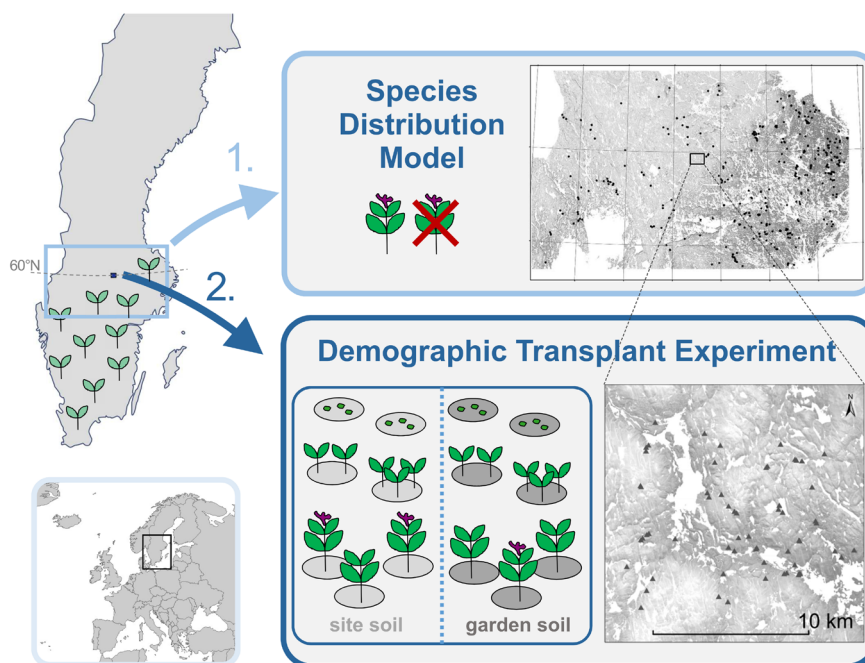


Figure 1. Study area and conceptual study design. Upper panel: first, we modelled the distribution of *Lathyrus vernus* across 52 409 km² of forested area at its cold range margin by relating presence–absence patterns to climate, light and soil variables. The map shows the presences as black dots. Lower panel: second, we tested in a transplant experiment the effects of climate, light and soil on the performance of *L. vernus* populations. The map shows the 58 transplant sites and schematic design of the experiment. At each site we planted adults, seedlings and seeds. Half of the plants at each site were planted in standard garden soil, half in original site soil.

vektor 1:25 000–1:10 000). We used the topographic wetness index (TWI) as an indirect measure for soil moisture (Sørensen et al. 2006). Lastly, to account for effects of land use we included forest age. Hypotheses for each variable are summarized in Table 1. All predictors were available as 50 m resolution raster files.

In the SDMs we used the following algorithms: generalized linear models (GLM), generalized additive models (GAM), boosted regression trees (generalized boosting models, GBM) and random forests (RF). These were combined in an ensemble model using the R package biomod2 (Thuiller et al. 2016). We used the true skill statistics (TSS, Allouche et al. 2006) and mean values of the area under the curve of a receiver operating characteristic plot to evaluate models (AUC, Fielding and Bell 1997). To assess the role of environmental variables, we computed their relative importance (Thuiller et al. 2009) and response curves for each model (more model details in Supplementary material Appendix 1). Finally, we projected the habitat suitability for the entire area using only models with a TSS score > 0.55 and weighting their contribution proportional to their TSS scores with the default weight decay of 1.6 (Thuiller et al. 2010).

Transplant experiment

For the transplant experiment, we did a stratified random selection to identify 58 sites within a 16×16 km area in the centre of the area used for the SDM (Fig. 1). We considered

the following factors in the site selection: microclimate, forest type and age, soil type and moisture (Supplementary material Appendix 1). At each of the sites, we transplanted six adults, ten juveniles and 60 seeds across an area of 5×5 m (Fig. 1, Supplementary material Appendix 2 Fig. A2). To further examine the effect of soil, half of the plants were placed in original site soil, and the other half in garden soil, the latter was expected to provide the better growing conditions compared to the original site soil (Supplementary material Appendix 1 and 2 Fig. A1).

Adult plants for the transplant experiment were raised from seeds from ten different populations in 2011 and 2012 and thereafter grown in a common garden (Dahlberg 2016). Seeds and seedlings originated from seeds collected in 2015 from a population in south-central Sweden (59°14'N, 17°16'E). Part of the intact seeds were used to raise seedlings in the greenhouse in 2016, and the remaining seeds were sown directly at our sites. The transplantation of adults and juveniles was carried out in April and May 2016. Seeds were sown in late July 2016, corresponding to the time of natural seed dispersal.

In June 2016, we recorded size (stem diameter and length of shoots), flowering status (flowering versus non-flowering) and number of fruits for all transplanted individuals. In June 2017, we recorded survival, size, flowering status, number of fruits, number of seeds per fruit and number and size of the seedlings that had established from the seeds sown in the first year (Supplementary material Appendix 1). Recruitment

Table 1. Predictor variables, their mean, range and underlying model hypothesis. Distributions of SDM predictors were estimated from the raster-grids, whereas distributions of the TE predictors were calculated from the 58 sites. SDM=species distribution model, TE=transplant experiment.

Approach	Variable	Hypothesis	Unit	Min	Mean	Max
SDM	growing degree days, GDD	at its cold range margin, the species prefers places with warm microclimate (= high GDD)	°C	751	1365	1658
SDM	solar radiation	at high latitudes with low sun angle during spring, the species may avoid topographically shaded sites	MW h ⁻¹ m ⁻²	0.45	0.66	0.77
SDM	proportion of conifers	species avoids pure conifer stands due to low litter/soil pH and dark forest floors in the spring	–	0	0.97	1
SDM	pH bedrock	species prefers base-rich soils	acidic, neutral, base rich	–	–	–
SDM	forest age	species is not found on clear cuts and not in very young forests, where it is outcompeted by fast-growing herbs	yr	0	54	170
SDM	topographic wetness index	species avoids very dry and very wet sites	–	8	12	26
TE	soil type	species responds positively to the standard garden soil and shows different responses to the other variables in the different soil types	garden soil, site soil	–	–	–
TE	canopy penetrating light	species prefers habitats with more canopy openness	%	23	44	78
TE	soil moisture	species avoids very dry and very wet sites	volume %	11	29	60
TE	growing degree days (April + May)	at its cold range margin, the species prefers places with warm microclimate (= high GDD)	°C	139	170	221
TE	freezing degree days (April + May), FDD	species doesn't like harsh frost conditions, i.e. prefers high FDD	°C	–100	–555	–25

probability was defined as the proportion of seeds sown in the first year that germinated the second year and were alive at the time of the recording. Growth was defined as the change in log-transformed size between two years, and size was defined as the sum of the products of basal area and length for each shoot ($((\text{diameter})^2 \times \pi/4 \times \text{length})$).

At each transplant site we took canopy cover photos after canopy closure (June 2016). Light was estimated by extracting the average percentage of white pixels from five binary canopy cover photos using the software ImageJ 1.50b (Abramoff et al. 2004). Soil moisture was measured in volume percent with a soil moisture meter (Delta-T Devices) at three locations per site during six dry days in September 2017. To adjust for differences among measurement days, moisture was also measured at a reference site each day. We used the adjusted average of the three measurements as a site value. We recorded temperature at each site every 3 h with two iButton loggers (type DS1921G-F5 and DS1923, Maxim Integrated, San Jose, CA, USA), at 5 cm and 1 m height. Loggers were protected from direct sun and rain (Supplementary material Appendix 2 Fig. A3). Daily minimum (T_{\min}) and maximum temperatures (T_{\max}) were calculated from the average of the two loggers at each site. We extracted two complementary microclimate indices: spring growing degree days (GDD) that describes favourability of growing conditions, and spring freezing degree days (FDD) that describes harmful frost conditions (Choler 2017, Supplementary material Appendix 1). Before modelling, all predictors were checked for collinearity with the Spearman rank coefficient (no coefficient smaller or larger than ± 0.50) and the variance inflation factor (no factor larger than 2).

Vital rate models

We estimated the effects of GDD, FDD, light, soil moisture and soil type on five vital rates (survival, growth, probability of flowering, number of seeds produced and recruitment probability), using generalized linear mixed effect models and site as a random effect in the R package lme4 (Bates et al. 2015). For survival, probability of flowering and recruitment probability, which were binary distributed, we used logit link functions, and for growth and number of seeds (square-root transformed), which were normally distributed, we used identity links. We included size in year 2016 as a predictor for survival, and size in 2017 as a predictor for probability of flowering and number of seeds in 2017. A quadratic term for size was added in the growth function to allow for non-linear relationships between previous and current size.

The initial full models included the five environmental variables and all two-way interactions of the four continuous variables with soil type. Models were reduced stepwise using the drop1 function in R. Model terms were kept when residual deviance could be reduced significantly, using a Chi-square test for model comparison (Zuur et al. 2009). In order to avoid excluding potentially important effects of environmental variables in the IPM, we used a relatively liberal criterion of $p < 0.1$ for inclusion of model terms. All variables were standardized (z-transformed) before

modelling, and importance of each variable was inferred from standardized model coefficients of the final models. We calculated the goodness-of-fit (R^2) for each model using the R package MuMIn (function r.squaredGLMM, Barton 2017), and extracted both the marginal R^2 , which includes only fixed effects, and the conditional R^2 , which includes both fixed and random effects.

Demographic model

Population growth rate, λ , was calculated using integral projection models (IPMs), which are an advancement of classical population matrix models, based on a continuous state variable rather than discrete classes (Easterling et al. 2000, Merow et al. 2014). We built an IPM for *L. vernus* based on standardized size as a state variable and the vital rate models identified by statistical models (Supplementary material Appendix 1). We calculated lambda over the observed range of each continuous environmental variable (100 equal distance levels), setting the other variables to their average. These calculations were done separately for both soil types. We compared the slopes of lambda over each environmental gradient to evaluate the impact on population growth rates. To assess the uncertainty of the lambda values, we bootstrapped the entire IPM-building procedure, including parametrizing the vital rate functions with the formula from the final model after model selection process. We bootstrapped a 100 times over sites with a sample size of 58 and assigned a pseudo-ID to each site-sample in order to be able to use the original formula with site as a random effect. Finally, we tested the correlation between predicted habitat suitability (log-transformed) from the SDM and population growth rates from the IPM, across the 58 sites and for both soil types.

All GIS work was done in ArcGIS ver. 10.4. All statistical analyses were done in R ver. 3.4.3 (R Core Team).

Results

Species distribution model

Habitat suitability for *L. vernus* decreased from SE to NW across the study area, and increased with higher GDD, lower proportion of conifers, older forests and higher pH (Fig. 2, Supplementary material Appendix 2 Fig. A5). GDD had the largest importance, followed by solar radiation, pH and proportion of conifers (Fig. 2). Habitat suitability was highest for low and high values of solar radiation. There was no clear correlation with TWI. The models had a good predictive quality with mean TSS scores of 0.52 ± 0.007 SE and mean AUC scores of 0.81 ± 0.003 SE (Supplementary material Appendix 2 Fig. A4). Model quality varied among algorithms and were usually slightly better for RF and GBM than for GLM and GAM.

Transplant experiment

Plants survived, grew and germinated better in garden soil than in natural soil (Fig. 3, Supplementary material Appendix

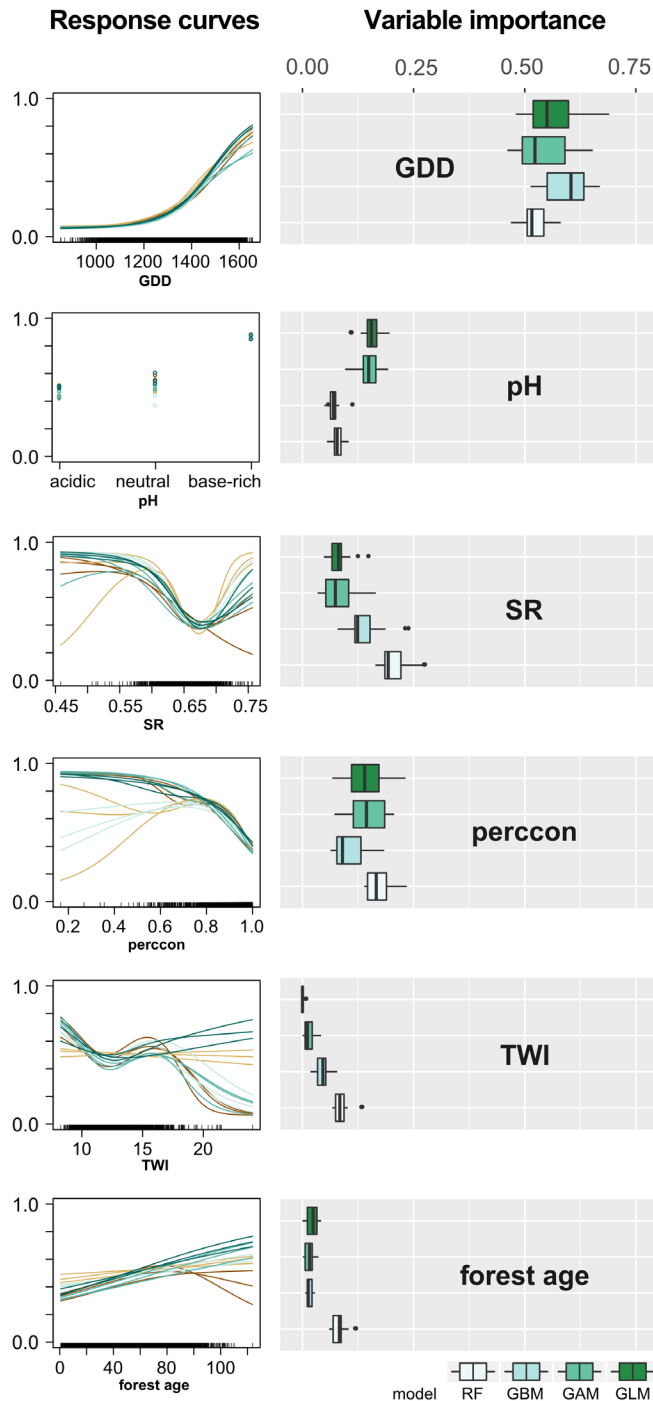


Figure 2. Examples of response curves (left) and relative importance (right) of five variables explaining presence/absence of *L. vernus* at its cold range margin using species distribution models. Relative importances are shown separately for each of the four model algorithms. Response curves are shown for the GAM models and observed predictor gradients (see main text for more details). Each colour in the response curve plots represents one of 15 separate model runs. GDD=growing degree days (base 5°C), SR=solar radiation in $\text{MW h}^{-1} \text{m}^{-2}$, pH=pH class of bedrock, percon=proportion of conifers, TWI=topographic wetness index, GLM=generalized linear model, GAM=generalized additive model, GBM=generalized boosting models, RF=random forest.

2 Fig. A6, Table A1). The effect of other environmental factors varied among vital rates, and differed between the two soil types. Light availability influenced survival and growth positively, but effects on growth were present only in garden soil. Higher soil moisture improved growth in both soils, but increased survival and tended to decrease the number of seeds and recruitment rate only in garden soil. FDD was positively related to survival in garden soil, and tended to be negatively related to the number of seeds. GDD tended to be positively correlated with growth in garden soil. All vital rates, except recruitment rate, increased significantly with increasing plant size (Supplementary material Appendix 2 Fig. A7). The variance explained by the vital rate models was high for growth (conditional $R^2=0.80$, marginal $R^2=0.75$), moderate for survival (0.51, 0.26), probability of flowering (0.51, 0.34) and number of seeds (0.45, 0.27), but lower for recruitment (0.06, 0.04).

Integrating the environmental effects via all vital rates showed that soil type and light conditions had large and interactive effects on population growth rate (Fig. 4). Populations growing on sites with more light performed better, particularly when growing in garden soil. Soil moisture had a moderate positive effect on lambda in site soil, but no effect in garden soil. FDD decreased lambda slightly in both soils. GDD had a weak positive effect on lambda, but only in garden soil (Fig. 4).

Correlation between habitat suitability and population growth rate

Habitat suitability predicted by the SDM was not correlated with the estimated population growth rate across the 58 transplant sites ($r=-0.15$, $p=0.27$ for site soil, and $r=-0.19$, $p=0.16$ for garden soil, Fig. 5).

Discussion

In this study, we used two different approaches to examine the environmental factors that limit a southern forest herb at its cold range margin. The SDM identified a strong effect of climate, while in the TE light and soil had larger effects on population growth rate than climate. Although both models agreed on the positive influence of warmer microclimate, there was no correlation between the predictions from the two approaches across the 58 sites. Below we discuss the results of each model, the reasons why results differed, and how the two approaches can complement each other.

Species distribution model

In concordance with the species' reported ecology and our hypothesis, *L. vernus* occurrences correlated strongly with a warmer climate (more GDD), more base-rich bedrock, older forest and less conifer trees. Growing degree days was the strongest predictor, suggesting that the species currently is climate-limited at its northern range margin. This finding agrees with strong climatic signals reported from distribution

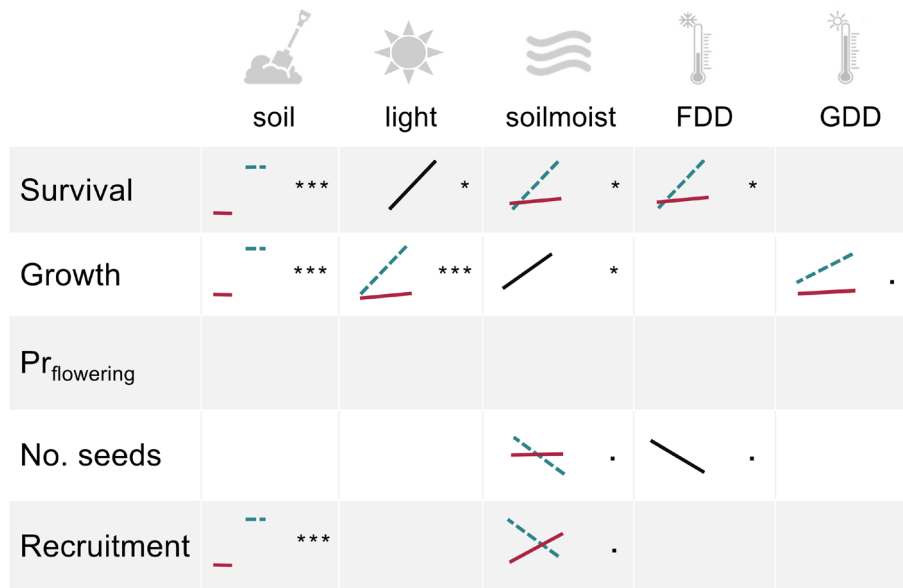


Figure 3. Summary of the environmental factors in the vital rate models (survival, growth, probability of flowering, number of produced seeds, recruitment probability). Red = site soil, green and dashed = standard garden soil, black = main effect when interaction with soil type was not significant. ' p < 0.1, '*' p < 0.05, '**' p < 0.01, '***' p < 0.001, direction and steepness of slopes indicate direction and strength of effects. Soil = soil type: either site soil (red) or standard garden soil (green), light = canopy openness, soilmoist = soil moisture, FDD = freezing degree days, GDD = growing degree days. Regression coefficients are provided in Supplementary material Appendix 2 Table A1.

models of many other species. For example, Normand et al. (2009) found that half of the investigated vascular plants were limited by temperature at their latitudinal and altitudinal upper range margin. Beauregard and De Blois (2016) reported that some investigated plant species at their cold

edge shifted to sites with warmer microclimate conditions. Still, we are cautious to infer climate limitation from the correlative SDMs, since many environmental variables as well as land use history in our study area change in parallel with climate (Ashcroft et al. 2011).

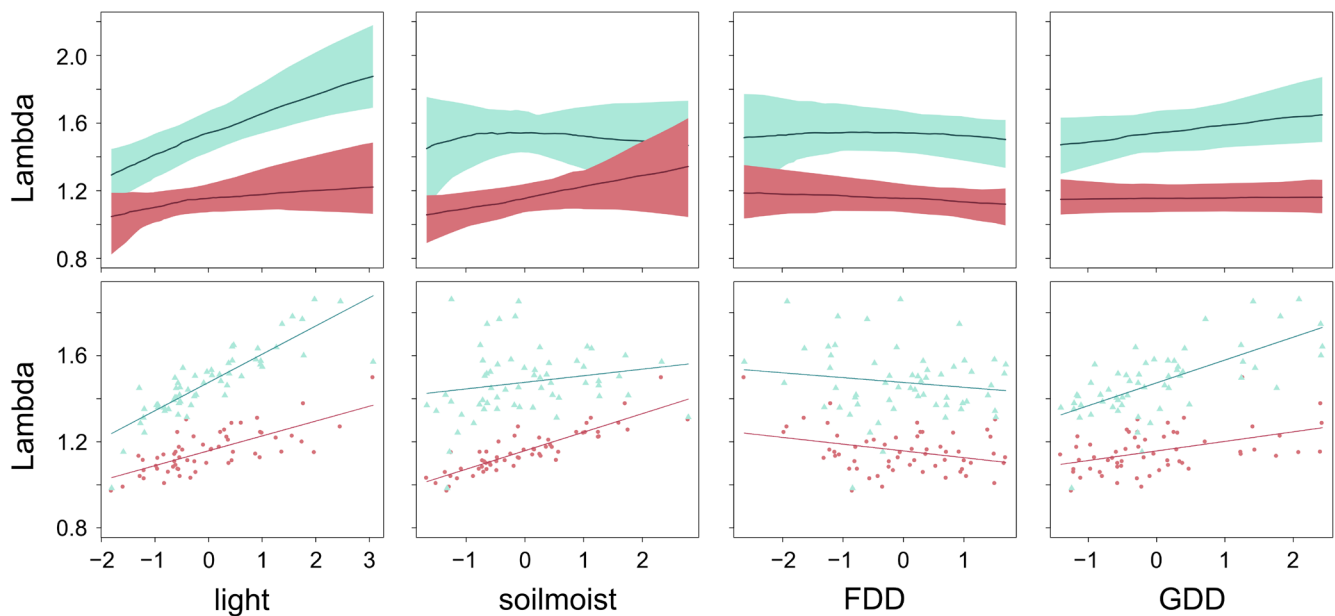


Figure 4. Effects of environmental factors (light, soil moisture, freezing degree days FDD, growing degree days GDD and their interaction with soil type) on the overall population growth rate measured as change in lambda, λ , over the observed range of one variable, while all others were set to their average. Light-green (triangles): standard garden soil. Red (circles): original site soil. All continuous variables are standardized. Upper panel: simulated lambda from bootstrapped models across all observed environmental gradients (median and 2.5th and 97.5th percentile). Lower panel: lambda for the 58 transplanted populations and imposed trend lines from single term linear regressions.

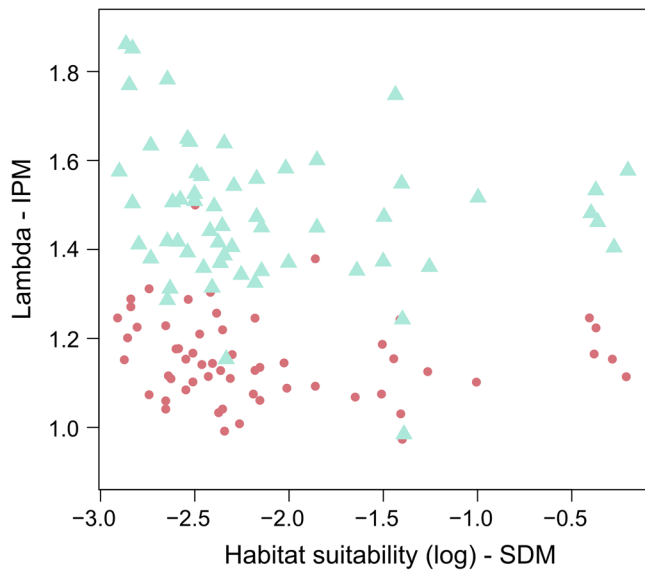


Figure 5. Relationship of population growth rate, lambda, derived from an integral projection model (IPM) and habitat suitability predicted by a species distribution model (SDM) for 58 transplanted populations growing in either standard garden soil (light-blue triangles) or original site soil (red circles) in otherwise natural habitats with contrasting microclimate, moisture and soil conditions.

Transplant experiment

In contrast to most previous transplant experiments, our design enabled us to investigate the effects of relatively long gradients of microclimate, light and soil conditions. Moreover, our experiment included multiple life stages and allowed us to calculate integrated measures of the effects on population performance. This is important since different vital rates might react in opposed directions to environmental variables. For example, freezing conditions (low FDD) had a negative effect on survival, but a positive effect on number of produced seeds. Our results thus serve as an illustration of the importance of integrating effects on all vital rates in geographic range studies (Merow et al. 2017, Pironon et al. 2018). Similar to many previous experiments, our study was of relatively short duration, implying that the absolute estimates of long-term population performance are uncertain, and that inferences have to be based on relative performance differences across sites.

Garden soil had a strong positive effect on population growth rate. Interestingly, the effect of the other environmental variables differed among soil types, being either weaker, as for soil moisture or stronger, as for light availability. This illustrates that interactive effects of environmental variables might often be important to understanding the factors determining distributions (Ehrlén et al. 2016).

Light availability also had a strong effect on population growth rate via effects on survival and growth. Several previous studies have shown that light availability may play a larger role than temperature gradients or nutrient availability on the forest floor (Flinn 2007, Baeten et al. 2010, De Frenne et al.

2015). Similarly, transplant experiments with other forest herbs have observed strong effects of soil and light conditions on plant performance (Meekins and McCarthy 2001, Van Der Veken et al. 2007). In boreal spruce-dominated forests, light conditions are likely to be particularly critical for light-demanding and early-flowering understory plants, because forest floors are dark and lack a shade-free period in the spring. Canopy-penetrating light is not only influencing photosynthetic active radiation, but also microclimate (Chen et al. 1993, Bramer et al. 2018, Greiser et al. 2018, Supplementary material Appendix 2 Fig. A8). A dense canopy buffers cold temperatures at night and warm temperatures during the day. Canopy cover also influences snow accumulation and ground frost during the winter (Storck et al. 2002).

Taken together, the results of the transplant experiment suggest that forest type, via effects on light and soil conditions, currently limit the species at its northern range margin and that direct effects of climate play a minor role. To the degree that climate controls the range of biomes and forest tree composition, which in turn can alter soil and light regimes, it is possible that *L. vernus* is indirectly limited by climate. If deciduous species with a more open canopy in spring and a higher bark pH (e.g. maple, ash) will track the warming front, more sites may eventually become suitable for the species. Given that the pattern observed during this study holds true also for a longer time period and that the climate conditions in that period were representative, the experimental populations seem to cope well with the climate at their current cold range margin.

How to reconcile the results of the two approaches?

The results from the SDM and TE approaches appear convincing when viewed separately, but still they did not produce a similar ranking of habitat quality across the 58 sites or a similar ranking of the importance of the environmental drivers. This might be associated with differences in both the predictors and the responses between the two models. Despite the fact that we used high-resolution spatial predictors, the variables used to describe climate, light and moisture were not correlated between the two approaches (Supplementary material Appendix 2 Fig. A9). While we were able to get accurate on-site measures of soil moisture, understory light and microclimate in the transplant experiment, similar information was lacking in a mapped format for the SDM. Moreover, the lengths of environmental gradients differed between the two approaches (Table 1). While the range in light and soil quality across sites and between treatments were larger in the transplant experiment, differences in climate variables were larger in the SDM. Taken together, this suggests that understory conditions were better described in the TE than in the SDM.

The SDM and the demographic TE also differed regarding the response against which the effects of environmental drivers were evaluated. The SDM predictions were based on occurrence data (presences), which reflect environmental conditions over several decades, while estimated population growth rates

in the transplant experiment reflect current conditions, measured during a single year. The SDM is thus more likely to have captured responses to long-term variation in important environmental drivers and rare events, like cold or dry years (but see Camarero et al. 2015), which can play an important role in determining cold range margins (Giesecke et al. 2010, Hargreaves et al. 2014, Lee-Yaw et al. 2016, Hoffmann et al. 2019). On the other hand, the long lifespan and poor dispersal of the study species implies that distributions might not yet have tracked recent changes in habitat suitability, such as climate warming. Conversely, current population growth rates estimated by the TE should not suffer from time lags, but also do not capture the effects of rare events. An additional difference is that while the SDM was based on natural populations, in the TE we used artificial populations where transplantation effects and planting design might have influenced performance. Based on all these differences in predictor and response variables between the two approaches, it is reasonable to assume that they capture different temporal and spatial aspects of the species' niche, and therefore, that their predictions could differ, but in informative and interpretable ways.

In line with this, the relatively high importance of soil type and moisture in the TE can be used to develop the interpretation of the SDM output, which captured well the gradient in habitat quality from southeast to northwest (Supplementary material Appendix 2 Fig. A5). This gradient is probably best represented by the climate variable, but also pH in the upper soil layer and the frequency of brown soils and deciduous forest patches change in parallel (SLU Markinfo 2019). Thus, the apparent limiting effect of climate in the SDM might also reflect an effect of low soil quality due to acidifying litter and declining sub-canopy light availability in increasingly conifer-dominated stands. Even historic land use changes along this axis with the south-east having a higher proportion of land that was under the plough or mowed before 1900 (Bernes 2011). Effects of differences in land use history might be partly captured by current conditions, such as the presence of broadleaved trees (Cousins and Eriksson 2001). However, the historic land use could also have influenced the distribution of *L. vernus* in ways not captured by current conditions, such as dispersal via transport of hay (Auffret et al. 2014). To account for such effects in the SDM, we would need gridded layers of different historical land use types, which currently are unavailable.

Contrary to our expectations, we found no correlation between the predicted habitat suitability (SDM) and the estimated population growth rate (TE) across the 58 sites. We have provided several possible explanations for this lack of correlation and among many possible avenues for future studies, two important questions spur from this study. The first is under which conditions the rank order of population growth rates yielded in short-term TEs are representative also of long-term growth rates. For example, while initial performance might have been driven largely by direct effects of environmental factors, the effects of competition might become increasingly important over time (Austin 1999). The second question is to what extent SDMs can be improved using a finer grid with better quality spatial predictors

(Potter et al. 2013, Lembrechts et al. 2018). Even if we used up-to-date high-resolution (50 m) predictors for several variables, we still lacked high-resolution data, for example, on soil pH. Moreover, small-scale variation in light, soil moisture and understory microclimate appeared not to have been well captured by our data.

To mitigate some of the problems associated with SDMs several approaches have been suggested to also incorporate vital rates and dispersal rates into these models (e.g. dynamic range models – Schurr and Pagel 2012, Schurr et al. 2012, and hybrid models – Thuiller et al. 2008, Dullinger et al. 2012). Another suggested approach is to use population growth and dispersal rates to predict distributions (Merow et al. 2011). While these and similar approaches are basically attempts to integrate multiple processes in a single modelling framework, the main point illustrated by our study is that results obtained through different approaches can provide complementary information leading to partly different inferences.

The relative strength and weaknesses of each approach will vary among study systems (Araújo and Peterson 2012, Schurr et al. 2012, Ehrlén and Morris 2015). For example, SDMs will be relatively more advantageous when environmental conditions are stationary, i.e. constant or stochastically varying, and when rare climatic events, unlikely to be captured during a transplant experiment, are important. On the other hand, TEs are likely to provide more accurate information when environmental conditions are changing, because time lags in responses to changes will be smaller for population growth rates than for extinctions and colonizations. SDMs are also likely to be particularly problematic for long-lived and poor-dispersed species, where we expect extinction and colonization time lags to be considerable. Lastly, from a methodological perspective, SDMs will be relatively more advantageous when information about putative environmental drivers is available in a mapped form and at a high spatial resolution, while TEs will be more useful when drivers are difficult to extract from map-based information.

Data availability statement

Plant demographic data and site data are available at <<https://doi.org/10.5061/dryad.8931zcrm8>> (Greiser et al. 2019).

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Supplementary material (available online as Appendix ecog-04490 at <www.ecography.org/appendix/ecog-04490>). Appendix 1–2.